Capitella caribaeorum sp. nov., a new capitellid polychaete from the Caribbean

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Introduction

The capitellid polychaete described below has been found intertidally amongst decaying mangrove leaves in southern Florida, Cuba and St Lucia. It forms a network of galleries, lined with mucus and faeces (Fig. 1a), through the surface layers of organic debris accumulated around mangrove roots. The worm has been cultured in agar through many generations (George, 1975) and its behaviour and life history have been elucidated from observations made both in the field and in the laboratory (George, 1984). Initially it was thought that the worm could be assigned to *Capitella giardi* (Mesnil, 1897), but subsequent study has shown that sufficient morphological, behavioural and physiological differences exist to warrant erection of a new species.

The description given below is based on adults collected from the natural habitat and supplemented by observations made on specimens from laboratory culture. No morphological differences were detected between worms from the wild populations and those from a culture that had been maintained in the laboratory for five years.

Specimens collected in the field were fixed in 10% neutralized commercial formalin in seawater for 48 hours before storage in 80% ethyl alcohol. Specimens derived from the cultures were either relaxed by slow addition of alcohol to seawater containing the worms prior to formalin fixation or were anaesthetized by slow addition of glutaraldehyde before fixation in 2·5% glutaraldehyde in 0·1 M phosphate buffer (pH 7·2) with 0·5 M sucrose. Material was dehydrated through the alcohols prior to examination by optical or scanning electron microscopy (SEM). Specimens to be examined by SEM (Hitachi S-800) were either air-dried using diethyl ether or acetone, or dried in an Edwards-Pearse tissue dryer—EPD3, using acetone and liquid CO_2, before coating with gold/palladium in a Polaron sputter coating unit.

Description of new species

Capitella caribaeorum sp. nov.

TYPES. The holotype is a fully grown specimen containing oocytes. The paratypes include specimens that have not reached physical maturity. The holotype (registration no. BM(NH) ZB. 1985. 191) and paratypes (registration nos. BM(NH) ZB. 1985. 192–196) are deposited in the collections of the British Museum (Natural History). Further paratypes have been deposited in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. and in the Australian Museum, Sydney.

TYPE LOCALITY. Southern Florida red mangrove (*Rhizophora mangle* Linnaeus) swamp, Matheson Hammock, Miami, Florida, U.S.A.

MORPHOLOGY. The species is small with fully grown individuals measuring up to 20 mm in length and 0·7 mm in width across the mid-thorax. The body is divided into a relatively muscular

thorax followed by a longer thinner abdomen which, unlike that of other capitellids such as *Mediomastus*, remains uncoiled when the worm is handled and when preserved (Fig. 1a). Living worms are light brown in colour and more or less transparent, at least in the abdominal region. Gravid worms show a distinctive banding pattern when stained with methyl green in alcohol (Banse, 1970). Segments 5–8 are stained all over, segment 4 shows only slight colouration and segment 9 does not take up the stain at all. As the stain is gradually washed out the sides of segments 7 and 8 retain the green colour longer than other parts of the worm. This staining pattern is less obvious in non-gravid individuals.

The prostomium is roughly conical, as broad at the base as it is long, and without a palpode. Its dorsal surface is flattened or slightly concave and there is a marked longitudinal ventral cleft (Fig. 1b). There are no obvious nuchal organs. Eyes are not visible in the adult, but a pair of eyes can be seen in a dorso-lateral position to the rear of the prostomium in larvae and recently metamorphosed juveniles.

The peristomium is about the same length as the prostomium but broader, with a large mouth situated ventrally (Fig. 1b). In living worms the demarcation between prostomium and peristomium is clearly visible, but in preserved material the distinction may be less obvious. There is a large eversible proboscis without obvious papillation.

There are nine thoracic chaetigers followed by an abdominal region with up to 40 segments. Thoracic segments are about three times as wide as long anteriorly, narrowing to twice as wide as long posteriorly. The surface is distinctly reticulated. There are no parapodial lobes, but there are widely separated notopodial and neuropodial chaetal bundles positioned half way to two-thirds back on each segment.

Both capillary chaetae and hooded hooks are present in the thorax. In fully grown worms chaetigers 1–6 bear capillaries exclusively in both notopodia and neuropodia. Chaetiger 7 typically has capillaries in the notopodia and hooded hooks in the neuropodia (Figs 1b; 2a). In chaetigers 8 and 9 there are no notopodial capillaries or hooded hooks; instead these segments bear stout genital hooks mid-dorsally and hooded hooks in the neuropodia (Figs 1c; 2a). This arrangement gives a thoracic chaetal formula of $1\text{–}6c\ 7^{C}_{H}\ 8\text{–}9^{G}_{H}$. However, this formula varies with age and size (see CHAETAL VARIATION).

The number of chaetae in any one bundle is small. There are usually 3 capillaries or 3 hooded hooks per bundle in the thorax (range 2–4) (Fig. 1b). Genital hooks develop in all individuals: usually 1–2 pairs point posteriorly on chaetiger 8 (Fig. 1c) and 1 pair points anteriorly on chaetiger 9. Older individuals have 3 pairs on chaetiger 8 and 2 pairs on chaetiger 9 but the second or third pairs are often very small (presumably replacements) and may be overlooked. The genital hooks on chaetiger 8 slightly overlap those on chaetiger 9 (Fig. 1c). The genital hooks surround a glandular pit similar to that found in male *Capitella capitata*.

The capillary chaetae are prominent. Using optical microscopy each capillary looks winged and has a distinct shoulder slightly above the exit point from the body. Using scanning electron microscopy it can be seen that the winged appearance is caused by the arrangement of the cylinders of which the chaeta is comprised (Figs 1d, e).

The hooded hooks are much shorter than the capillaries and only protrude a short way from the body (Fig. 3a). They each have a shoulder like that of the capillary chaeta, but in this case the shaft terminates in a pointed hook surrounded by a hood which is transparent in transmitted

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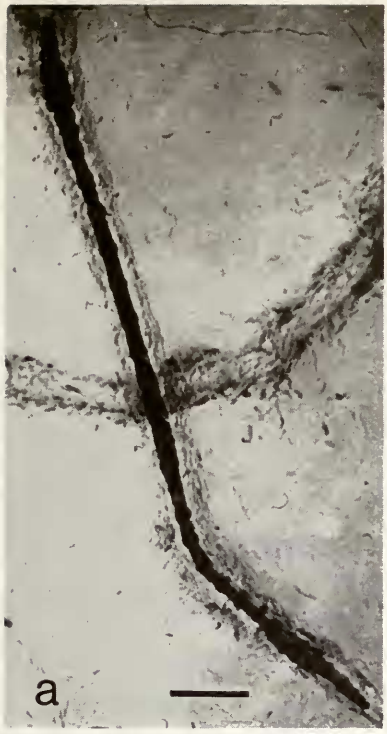
Fig. 1. a: A living adult of *Capitella caribaeorum* showing the general body proportions. The worm is in its burrow which is lined with mucus and faecal pellets (scale bar = 1·5 mm). b: Ventro-lateral view of the head and thorax of an adult. A few segments of the posterior part of the abdomen are also visible, lying alongside the anterior end (scale bar = 130 μm). c: A lateral view of part of the thorax of a sexually mature worm showing the dorsally situated, backwardly pointing, genital hooks of chaetiger 8. (The forward pointing genital hooks of chaetiger 9 are obscured from view) (scale bar = 60 μm). d: Three capillary chaetae of a thoracic notopodium (scale bar = 25 μm). e: A lateral view of two capillary chaetae showing details of their construction (scale bar = 7 μm). (Fig. 1a, transmitted light photograph; Figs. 1b–e, scanning electron micrographs).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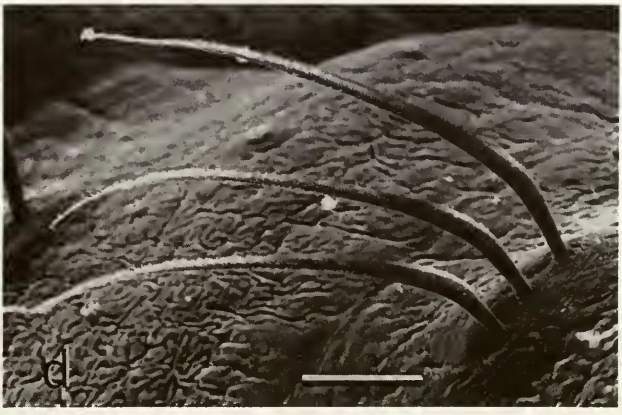
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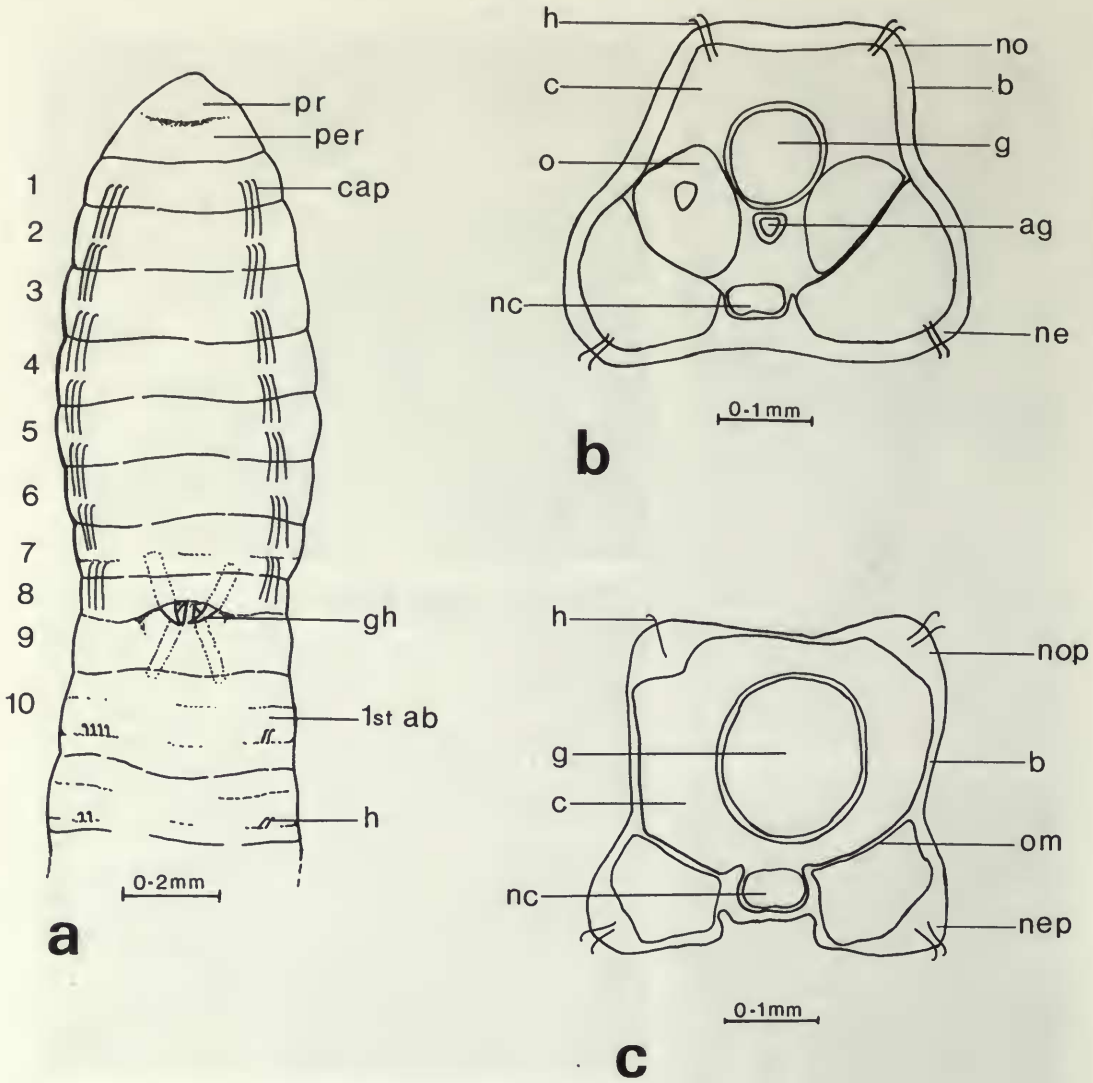
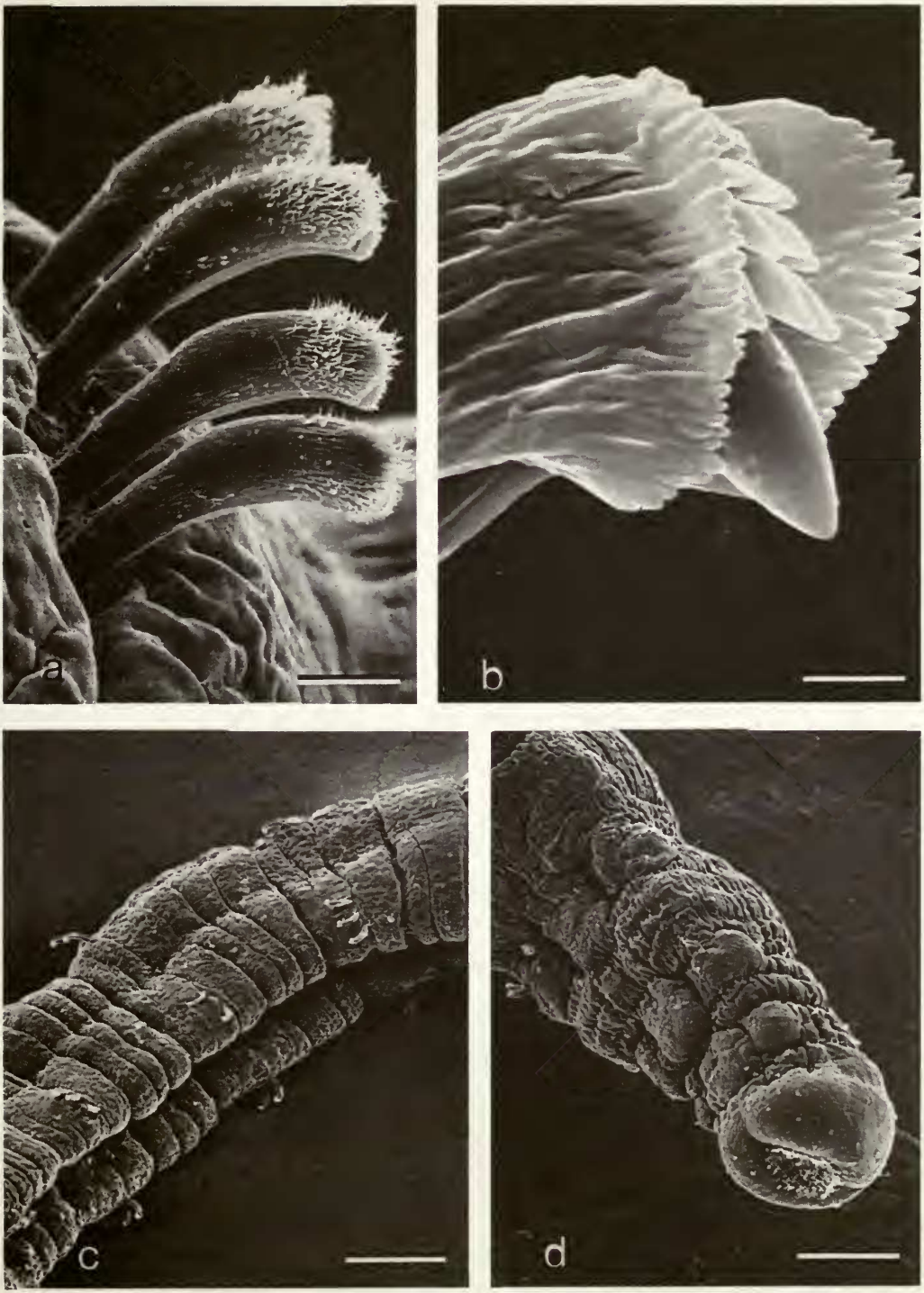


Fig. 2. a: Dorsal view of anterior end showing arrangement of thoracic chaetae. b: TS through an anterior abdominal segment. c: TS through a posterior abdominal segment. ag—accessory gut; b—body wall; cap—capillary chaeta; c—coelom; g—gut; gh—genital hook; h—hooded hook; nc—nerve cord; ne—neuropodium; nep—neuropodial pad; no—notopodium; nop—notopodial pad; o—oocyte; om—oblique muscle; per—peristomium; pr—prostomium; 1st ab—first abdominal segment. Numbers refer to chaetiger number.

Fig. 3. a: A bundle of four hooded hooks protruding from the body wall (scale bar = 7 μm). b: Detail of the head of a hooded chaeta showing the main fang-like tooth overlain by smaller teeth (scale bar = 1 μm). c: A view of the abdomen showing the rectangular box-shaped segments with widely spaced bundles of chaetae (scale bar = 85 μm). d: The posterior end of the body showing the glandular pygidium and the area of segment proliferation immediately in front of it (scale bar = 65 μm). (Figs. 3a–d, scanning electron micrographs).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light. Using scanning electron microscropy it can be seen that the hood consists of several layers of small diameter cylinders which form the outer layer of the chaeta below the shoulder (Fig. 3a). The hook itself is comprised of a large fang-like tooth overlain by several rows of smaller teeth (Fig. 3b). The fang and teeth are the ends of the larger cylinders forming the core of the chaeta. The number and arrangement of the teeth as viewed using light microscopy are not reliable taxonomic characters.

As in most capitellids the junction of thorax and abdomen is not always clearly defined externally, although the groove between segments 9 and 10 is usually more obvious than grooves between preceding thoracic segments. Abdominal segments are thin-walled and transparent when compared with those of the thorax in both living and preserved animals (Fig. 1a). The anterior abdominal segments are about the same length as posterior thoracic ones and are at least as long as wide, but the length:width ratio increases posteriorly until segments become two to three times longer than wide. In cross section the anterior abdominal segments are roughly triangular (Fig. 2b), but posterior ones are more like squares, with each segment looking like a rectangular box (Figs 2c; 3c).

Table 1. Thoracic chaetal formulae in a sample of *Capitella caribaeorum* collected from southern Florida

Formula				No. of individuals
1–3C	4–9H			3
1–3C	4^{C}_{H}	5–9H		1
1–4C	5^{C}_{H}	6–9H		7
1–4C	$5–6^{C}_{H}$	7–8H	9^{G}_{H}	1
1–5C	6–7H	$8–9^{G}_{H}$		1
1–5C	6^{C}_{H}	7–9H		1
1–5C	6^{C}_{H}	7H	$8–9^{G}_{H}$	9
1–5C	$6–7^{C}_{H}$	$8–9^{G}_{H}$		2
1–6C	7H	$8–9^{G}_{H}$		2
1–6C	$7^{C'H}_{H}$	$8–9^{G}_{H}$		1
1–6C	7^{C}_{H}	$8–9^{G}_{H}$		5
1–7C	$8–9^{G}_{H}$			1

C, capillaries only in notopodia and neuropodia; H, hooded hooks only in notopodia and neuropodia; $\frac{C}{H}$, capillaries only in notopodia, hooded hooks only in neuropodia; $\frac{C/H}{H}$, mixed bundles of capillaries and hooded hooks in notopodia, hooded hooks only in neuropodia; $\frac{G}{H}$, genital hooks only in notopodia, hooded hooks only in neuropodia.

Data on total length and chaetiger number are not included because some specimens had rear ends missing. It is important to note that the relative frequency of individuals with any particular chaetal formula will vary according to the age structure of the population. This table merely gives an indication of the range of formulae to be encountered in a sample of worms.

Chaetae are arranged in four widely-spaced bundles situated to the rear of each segment (Fig. 3c). In posterior segments the chaetae arise from glandular pads of which the neuropodial ones are more obvious (Fig. 1b). All abdominal segments normally bear chaetae (an average of two per bundle) except for developing segments in front of the pygidium (Fig. 3d). All abdominal chaetae are hooded hooks that are similar in structure to those found on the thorax.

The body terminates as a prominent glandular pygidium which takes the form of a swollen ring partly divided into two lobes by a posteroventral cleft containing the anus (Fig. 3d).

In gravid forms large yolky eggs are visible from segment 11. The number of ovigerous segments increases with age, ranging from eleven to thirteen. In young worms each ovary contains a single oocyte, but this number may increase to two or three in older worms. The species is hermaphroditic and under laboratory conditions is capable of self-fertilization (George, 1984).

CHAETAL VARIATION. George (1984) has traced the development of this species from larva to mature adult. At metamorphosis only the first 3 chaetigers have capillary chaetae; all others bear hooded hooks exclusively. At this stage there are 13 chaetigers. With increasing age capillaries gradually replace the hooks progressively backwards along the thorax. When the worms reach the 27–33 chaetiger stage there are only capillaries on segment 5, with mixed bundles of capillaries and hooded hooks on segment 6 and sometimes segment 7. At about this stage the genital hooks begin to develop and eventually the notopodial hooded hooks of segments 8 and 9 drop out.

Table 1 records the range of thoracic chaetal formulae of a field sample of 35 worms. The table gives some indication of the variation likely to be encountered in a natural population of this species. Such variability makes the use of thoracic chaetal formulae as a character for identification purposes very unreliable if used in isolation. However, there is a clear relationship between

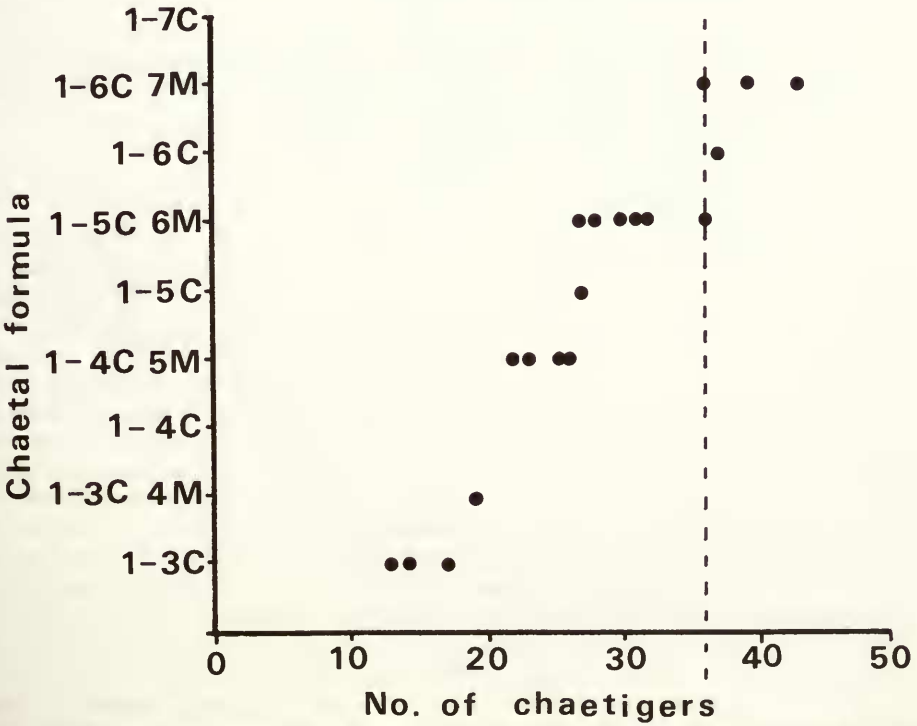

Fig. 4. Relationship between thoracic chaetal formula and chaetiger number in a sample of complete specimens. C—segment with capillaries only; M—segment with capillaries and hooded hooks. George (1984) found that no worms with fewer than 36 chaetigers were gravid. The 36-chaetiger point is indicated by a dotted line in the figure.

thoracic chaetal formula and total number of chaetigers as can be seen by analysis of a sample of complete worms (Fig. 4). Whenever possible, therefore, identifications should be based on a large sample of worms, including many complete individuals, and the relationship between thoracic chaetal formula and total chaetiger number checked against Fig. 4.

Discussion

Four genera of capitellids with nine thoracic chaetigers and genital hooks have been described. Of these *Branchiocapitella* Fauvel, 1932 is readily distinguished by the presence of cirriform branchiae. Warren (1976) referred *Capitellides* Mesnil, 1897 to the genus *Capitella* Blainville, 1828. *Capitellides* had been distinguished principally by the presence of genital hooks in both sexes. The description of *Capitomastus* Langerhans, 1880 is also very similar, but it includes reference to sexual dimorphism in the thoracic chaetal formula. The relationships of these three genera are very uncertain and a reappraisal of the *Capitella*/*Capitellides*/*Capitomastus* complex is currently under investigation by one of us (LMW).

Capitella caribaeorum appears to have many morphological and developmental features in common with *Capitomastus minimus sensu* Hauenschild (1954) collected from Rhodes in the Mediterranean. In the absence of either a detailed description or reference material it is impossible to draw any firm conclusion as to the status of this material.

Four species of *Capitella* with genital hooks in ovigerous individuals have been described. Of these *Capitella* (= *Capitellides*) *jonesi* (Hartman, 1959) and *Capitella* (= *Capitellides*) *teres* (Treadwell, 1939) have been recorded from the Caribbean province. Neither of these, however, could be confused with *C. caribaeorum* as they have different thoracic chaetal formulae: in *C. caribaeorum* the capillary chaetae occur in the first six or seven segments, whereas in *C. jonesi* they are restricted to the first three segments and in *C. teres* are present on the first eight segments.

In *Capitella hermaphrodita* Boletzky and Dohle, 1967 not all adults possess genital hooks and there are indications of a sex change from female to male (Warren, 1976). In *C. caribaeorum* the male reproductive system develops in advance of the female (George, 1984). Furthermore, capillary chaetae occur only on the first four chaetigers in *C. hermaphrodita*.

C. caribaeorum is most similar to *Capitella* (= *Capitellides*) *giardi* which was first described from the northern coast of France. The thoracic chaetal formula of this species is 1–6c 7_H $8–9^G_H$, although capillaries are sometimes present in segment 7, giving it an identical formula to that of *C. caribaeorum*. *C. caribaeorum* differs most markedly in the number of hooded hooks, having on average 3 hooks per bundle in the thorax and 2 per bundle in the abdomen, whereas *C. giardi* has 4–5 hooks per bundle in the thorax and 7–10 per bundle in the abdomen. Adult *C. giardi* are slightly smaller than *C. caribaeorum* (Mesnil quoted a length of 10 mm) with a comparable number of chaetigers (35–45) so these differences cannot be attributed to size variations. Like *C. caribaeorum*, *C. giardi* produces a few large eggs. Mesnil (1897) quoted a dimension of 500 μm and Day (1937) gave a range of 290–370 μm for the largest dimension, compared with an average of 300 μm for *C. caribaeorum* (George, 1984). Although the egg sizes are similar, Day, in his description of the development of *C. giardi*, reported that at metamorphosis larvae had the first three segments with capillaries followed by thirteen segments with hooks. *C. caribaeorum*, on the other hand, has three segments bearing capillaries followed by ten hooked segments at metamorphosis (George, 1984). There is no evidence in the literature that *C. giardi* is hermaphroditic.

There are marked ecological differences between these two species. Mesnil found *C. giardi* in the intertidal zone at Wimereux in sediment covering clayey rock accompanied by *Polydora ciliata* (Johnston, 1838), *Pygospio elegans* Claparède, 1863 and *Fabricia sabella* (Ehrenberg, 1837), and amongst a thick encrustation of *Lithothamnion polymorphum* (Linnaeus) in rock pools in the granite bedrock at St Martin's Bay near to Cap de la Hague (n.b. It is unlikely that the species forming encrustations was *L. polymorphum* as stated by Mesnil. It is more likely to have been *Lithophyllum incrustans* Philippi). This is in marked contrast to the habitat of *C. caribaeorum* amongst decaying mangrove leaves.

George (1975) investigated the effects of temperature on the development of *C. caribaeorum* and found that 10°C was near the lower lethal limit for the species. At 15°C adults survived, but larvae did not develop beyond metamorphosis. The occurrence of *C. giardi* on the north coast of France indicates that this species survives far lower temperatures in the winter months.

In view of the apparent physical similarity between the species we attempted to obtain the type material of *C. giardi*, but this could not be traced. We made collections at both of its type localities in order to try to obtain specimens for comparison with *C. caribaeorum* but were unsuccessful.

Differential diagnosis

Capitella caribaeorum sp. nov. may be distinguished from the other species in the genus by the following characters: length 20 mm; 50 chaetigers; thoracic chaetal formula 1–6c 7^{C}_{H} 8–9^{G}_{H}; average of 3 chaetae per bundle in thorax, 2 per bundle in abdomen; hermaphroditic; habitat—decaying mangrove leaves; distribution—Caribbean province.

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References

Banse, K. 1970. The small species of *Euchone* Malmgren (Sabellidae, Polychaeta). *Proceedings of the Biological Society of Washington* **83:** 387–408.

Day, J. H. 1937. The development of *Capitellides giardi* Mesnil. *Report of the Dove Marine Laboratory* **4:** 31–37.

George, J. D. 1975. The culture of benthic polychaetes and harpacticoid copepods on agar. *10th European Symposium on Marine Biology, Ostend, Belgium, Sept. 17–23, 1975* **1:** 143–159.

—— 1984. The behaviour and life history of a mangrove-dwelling capitellid (Polychaeta). *In*: Hutchings, P. A. (Ed.) *Proceedings of the First International Polychaete Conference*. Sydney (The Linnean Society of New South Wales): 323–337.

Hauenschild, C. 1954. Über Sexualität und Entwicklungszyklus von *Capitomastus minimus*. *Zoologische Jahrbücher* **65:** 54–58.

Mesnil, F. 1897. Note sur un Capitellien nouveau (*Capitellides* n. gen., *Giardi* n. sp.). *Zoologischer Anzeiger* **20:** 441–443.

Warren, L. M. 1976. A review of the genus *Capitella* (Polychaeta: Capitellidae). *Journal of Zoology* **180:** 195–209.

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